THE EVOLUTION OF THE HETEROMYARIAN
CONDITION IN THE DREISSENACEA
(BIVALVIA)

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ABSTRACT. Inspection of the valves of living members of the Corbiculacea and Dreissenacea and fossil Dreissenacea in the collections of the British Museum (Natural History) has revealed that the evolution of the heteromyarian form in present-day Dreissenacea in all probability arose from an established isomyarian corbiculid stock.

Descriptions of the taxa examined are given, and the stages in the evolution of the Dreissenacea discussed.

Dreissena polymorpha Pallas was first encountered in the River Volga and the Black Sea in 1754 by Pallas, who being struck by the superficial similarity of the animal to members of the Mytilacea named it *Mytilus polymorphus*. In 1835 Van Beneden established that it differed fundamentally from true mytilids and suggested the generic name *Dreissena*. Gray (1840) was responsible for separating *Dreissena* even further from the mytilids by suggesting that it should be placed in a separate superfamily, the Dreissenacea.

Toureng (1894*a*, *b*) showed, on the basis of the structure of the central nervous system and blood vascular system that *Dreissena* was not related to *Mytilus*, whilst Atkins (1937) and Purchon (1960) respectively showed that on the basis of the structure of the ctenidia and stomach the Mytilacea and Dreissenacea are unrelated. Yonge and Campbell (1968) showed that *Dreissena* is very different from the mytilid *Septifer* which has, like *Dreissena*, its anterior adductor muscles inserted on a shell shelf situated near the umbo. It is now generally considered that the similarities which exist between *Dreissena* and the Mytilacea are the result of convergent evolution of the heteromyarian condition in the two groups.

The possession by *Dreissena* of so many anatomical features that are typically 'eulamellibranch' (Morton 1969*a*) suggests that the close relatives of *Dreissena* should not be sought amongst the 'filibranch' bivalve phylogenies but amongst other eulamellibranchs. Taylor *et al.* (1970) have shown that on the basis of the microstructure of the shell, *Dreissena* is most like members of the Corbiculacea. This observation supports the grouping by Newell (1965) of the Dreissenacea with, amongst others, the Corbiculacea in the suborder Articina.

Fossil Dreissenacea in the collections of the British Museum (Natural History) and present day Dreissenacea and Corbiculacea were studied to discover if there is any evidence for the hypothesis of a common ancestry between the isomyarian Corbiculacea and the anisomyarian Dreissenacea. The methods of classification of the Bivalvia (Newell 1965) and of the Dreissenacea adopted by Keen (1969) are used in this paper.

To facilitate discussion of the evolutionary history of the Dreissenacea, short descriptions and simple figures of the left valves of some of the taxa examined follows.

DESCRIPTION OF SHELLS

Superfamily DREISSENACEA Gray *in* Turton 1840
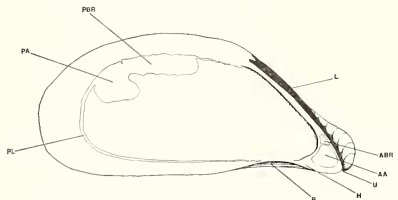Family DREISSENIDAE Gray *in* Turton 1840 (ICZN No. 76)

Genus DREISSENA Beneden 1835 (ICZN No. 872)

Subgenus *Dreissena* s.s.
Dreissena (*Dreissena*) *polymorpha* (Pallas)

Text-fig. 1

Material. A large collection of recent specimens from reservoir No. 2, Walthamstow, London.

TEXT-FIG. 1. *Dreissena polymorpha*. Interior view of left valve. (For key to lettering see p. 571.)

Description. Shell solid, slightly inequivalve; inequilateral, beaks in anterior half; subtriangular, elongated and swollen; flattened ventrally, with byssal notch anteriorly. Specimens up to 5·0 cm. in length. No internal nacreous layer, ligament internal, extending along dorsal line less than $\frac{1}{2}$ distance of posterior margin. Hinge plate without teeth. Anterior adductor and anterior byssal retractor muscles located on hinge plate, adjoined to each other. Anterior adductor smaller than posterior; pallial line not indented by sinus. Margin smooth; growth rings well defined; colour yellowish or brown, marked with zigzag alternating bands of brown and yellow.

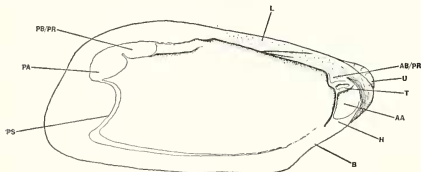*Mode of life.* Byssally attached, epifaunal, in shallow fresh and estuarine waters.

Range. Eocene—Recent. Old World.

Subgenus *Dreissenomya* Fuchs 1870
Dreissena (*Dreissenomya*) *aperta* (Deshayes) 1836

Text-fig. 2

Material. One specimen from the Upper Tertiary, Pontian (Bosphorian) of the Stoichitza valley, Cocorova-Mehedintzi, Rumania. BMNH LL 18451.

TEXT-FIG. 2. *Dreissena* (*Dreissenomya*) *aperta*. Interior view of left valve. (For key to lettering see p. 571.)

Description. Shell solid, equivalve; inequilateral, beaks in anterior half; tending to be rectangular or broadly oval with posterior margins rounded, enlarged and gaping. Well-defined byssal notch anteriorly; specimen 2·5 cm. in length. No internal nacreous layer to shell. Ligament internal, extending along dorsal line $\frac{1}{2}$ distance of posterior margin. Hinge plate with two rudimentary cardinal teeth. Anterior adductor and anterior byssal and/or anterior pedal retractor muscle scars located on hinge plate on each side of and closely adjoined to cardinal teeth. Anterior and posterior adductor muscle scars of approximately equal size; pallial line with well-defined sinus. Margin smooth.

Inferred mode of life. Bysally attached, infaunal, siphonate, apparently associated with such non-marine forms as *Theodoxus* and the aberrant non-marine Cardiacea. In fresh and estuarine waters.

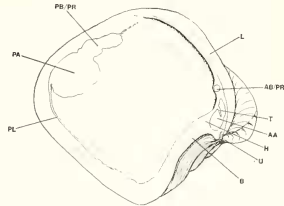*Range.* Miocene–Pliocene. Old World.

Genus CONGERIA Partsch 1885

Congeria subglobosa Partsch

Text-fig. 3

Material. One specimen from the Miocene of Nussdorf, near Vienna. BMNH L22134.

Description. Shell solid, equivalve; inequilateral, beaks in front of mid-line directed forwards; angular, nearly square in outline. Specimen 8·5 cm. long; no internal nacreous layer to shell. Ligament internal, extending along dorsal line almost $\frac{1}{2}$ length of posterior margin. Growth-lines distinct, well-defined byssal notch. Hinge plate with single poorly developed cardinal tooth, covered in life by anterior adductor muscle. Anterior byssal and/or anterior pedal retractor muscle scar also located on hinge plate, posterior to anterior adductor muscle scar. Anterior adductor muscle scar smaller than posterior. Pallial line not indented by sinus. Margin smooth.

TEXT-FIG. 3. *Congeria subglobosa.* Interior view of left valve. (For key to lettering see p. 571.)

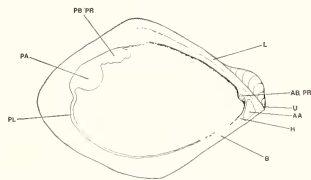*Inferred mode of life.* Bysally attached, infaunal, in fresh and estuarine waters.

Range. Oligocene–Pliocene. Old World.

Congeria zsigmondyi Halad

Text-fig. 4

Material. Eleven specimens from the Miocene of Sangenfeld, Temes, Hungary. BMNH L71758–68.

Description. Shell solid, equivalve; inequilateral, beaks in anterior half; angular, rhomboidal in outline. Specimen 2·5 cm. in length; no internal nacreous layer to shell. Ligament internal extending along dorsal line $\frac{1}{2}$ distance of posterior margin. Byssal notch anteriorly. Hinge plate without teeth. Anterior adductor and anterior byssal and/or anterior pedal retractor muscles located on hinge plate, latter posterior to anterior adductor and having its insertion on 'hinge lobe' projecting down from hinge plate. Anterior adductor muscle scar smaller than posterior. Pallial line not indented by sinus. Margin smooth.

TEXT-FIG. 4. *Congeria zsigmondyi.* Interior view of left valve. (For key to lettering see p. 571.)
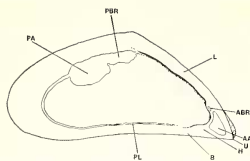
Inferred mode of life. Byssally attached, infaunal, in fresh and estuarine waters.

Range. Oligocene–Pliocene. Old World.

Congeria subcarinata botenica Andrusov

Text-fig. 5

Material. A single specimen from the Miocene of the Pricăles valley, Susitza-Mehedintzi, Rumania. BMNH, unregistered.

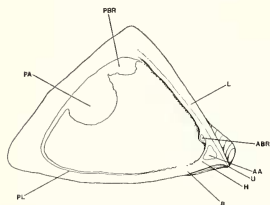TEXT-FIG. 5. *Congeria subcarinata botenica*. Interior view of left valve. (For key to lettering see p. 571.)

Description. Shell solid, equivalve; inequilateral, beaks in anterior half; approximately triangular in outline, flattened ventrally and with anterior byssal notch. Specimen 5·5 cm. in length. No internal nacreous layer to shell. Ligament internal, extending along dorsal line almost $\frac{1}{2}$ distance of posterior margin. Hinge plate without teeth. Anterior adductor and anterior byssal and/or pedal retractor muscles located on hinge plate, latter posterior to anterior adductor. Anterior adductor muscle scar smaller than posterior. Pallial line not indented by sinus. Margin smooth.

Inferred mode of life. Byssally attached, epifaunal, in fresh and estuarine waters.

Range. Oligocene–Pliocene. Old World.

Congeria triangularis Partsch

Text-fig. 6

Material. Four specimens from the Miocene, Pontian of Radmanest, Krasso, Hungary. BMNH L71686–9.

TEXT-FIG. 6. *Congeria triangularis*. Interior view of left valve. (For key to lettering see p. 571.)

Description. Shell solid, equivalve; inequilateral, beaks in anterior half; sharply triangular in outline, flattened ventrally and with anterior byssal notch. Specimen 4·0 cm. in length. No internal nacreous layer to shell. Ligament internal, extending along dorsal line almost $\frac{1}{2}$ distance of posterior margin. Hinge plate without teeth. Anterior adductor and anterior byssal and/or pedal retractor muscles located on hinge plate, latter posterior to anterior adductor and having its insertion on 'hinge lobe' projecting down from hinge plate. Anterior adductor muscle scar much smaller than posterior. Pallial line not indented by sinus. Growth-lines distinct. Margin smooth.
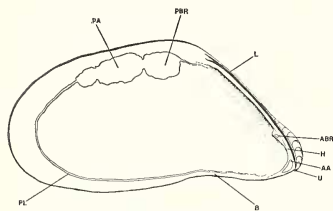
Inferred mode of life. Byssally attached, epifaunal, in fresh and estuarine waters.

Range. Oligocene–Pliocene. Old World.

Genus MYTILOPSIS Conrad 1858

Mytilopsis sallei (Recluz)

Text-fig. 7

Material. A large collection of recent specimens from Visakhapatnam harbour, India, where they seem to have recently been introduced from Central America.

TEXT-FIG. 7. *Mytilopsis sallei*. Interior view of left valve. (For key to lettering see p. 571.)

Description. Shell brittle, equivalve; inequilateral, beaks in anterior half; subtriangular, elongated, not swollen; slightly flattened ventrally, convex dorsally. Well defined byssal notch anteriorly. Specimen 1·4 cm. in length. No internal nacreous layer to shell. Ligament internal, extending along dorsal line less than $\frac{1}{2}$ distance of posterior margin. Hinge plate without teeth. Anterior adductor and anterior byssal retractor muscles inserted on hinge plate, latter posterior to anterior adductor and having its insertion

on 'hinge lobe' projecting down from hinge plate. Anterior adductor muscle scar smaller than posterior. Pallial line not indented by sinus. Margin smooth.

Mode of life. Byssally attached, epifaunal, in shallow estuarine and sea waters.

Range. Upper Oligocene–Recent. Central America and India.

Other species in the genus *Mytilopsis* include:

Mytilopsis leucophaeta Conrad	Eastern North America.
Mytilopsis cochleata Kickx	Northern Europe.
Mytilopsis africanus Beneden	West Africa.

All the above mentioned species bear a very close resemblance to *M. sallei* and for this reason are not described or illustrated.

DISCUSSION

One of the most characteristic features of the shell of *Dreissena* (text-fig. 1) is the possession of a shell shelf upon which is inserted the anterior adductor muscle and the anterior byssal retractor muscle. Amongst other bivalves the same type of structure occurs in the Mytilid genus *Septifer*, although in this genus only the anterior adductor muscle has its insertion upon the shelf (Yonge and Campbell 1968). It has been suggested by Yonge and Campbell (1968) that the possession of this structure in these two stocks is the result of convergent evolution by adaptation to similar modes of life. It would seem that the forward extension of the umbones and the extremes of ventral (morphologically anterior) flattening in these two species has necessitated the evolutionary development of an anchorage, other than the valve itself, for the anterior adductor muscles. Yonge and Campbell pointed out that the possession of this shelf in these two genera not only permits the retention of the anterior adductors but enhances their function. They also suggested that the formation of the shell shelf in these two genera was achieved by a pushing forward of the mantle tissues in the region just within the area of insertion of the anterior adductors. This process (although perhaps only occurring in isolated instances in the Mytilacea, e.g. *Septifer*) is a feature of all fossil and living Dreissenacea. It is suggested that the shell shelf in the Dreissenacea has a deep evolutionary significance and is homologous to the hinge plate of other bivalves.

Taylor *et al.* (1970) showed that the detailed structure of the shell of *Dreissena polymorpha* most closely resembles that of certain corbiculids. Inspection of fossil Dreissenacea similarly suggests the possibility of a common ancestry for these two groups of bivalves.

Each valve of *Corbicula* possesses two adductor muscle scars of approximately equal size and two smaller pedal retractors. The shell is equilateral, with a small internal ligament, and three cardinal teeth lying on the hinge plate immediately below the umbo (text-fig. 8A). In another corbiculid, *Villorita cyprinoides*, the first signs of anterior flattening are seen, accompanied by extension of the ligament and posterior region of the shell. This has resulted in this species in the reduction of the anterior portion of the hinge plate and the movement of the anterior adductor and pedal retractor muscles towards the umbo. The extension of the dorsal (posterior) region of the shell has resulted in the greater development of the posterior adductor and pedal muscles, relative to the anterior muscles (text-fig. 8B).

Yonge (1962) showed that bivalves in many phylogenies have retained into adult life an essentially larval characteristic, the byssus, and that the neotenous retention of

this structure has, in many cases, influenced the form of the shell. The effect of the
retention of the byssus in forms essentially similar to present-day *Villorita* would have
been to produce forms in which the processes of ventral flattening were extreme, neces-
sitating not only a change in mode of life but also of function of some organ systems.
The fossil record shows some Driessenacea in which these changes can be observed;
and although these forms have become extinct, it is suggested that they may represent
stages through which the ancestors of present-day Dreissenacea passed.
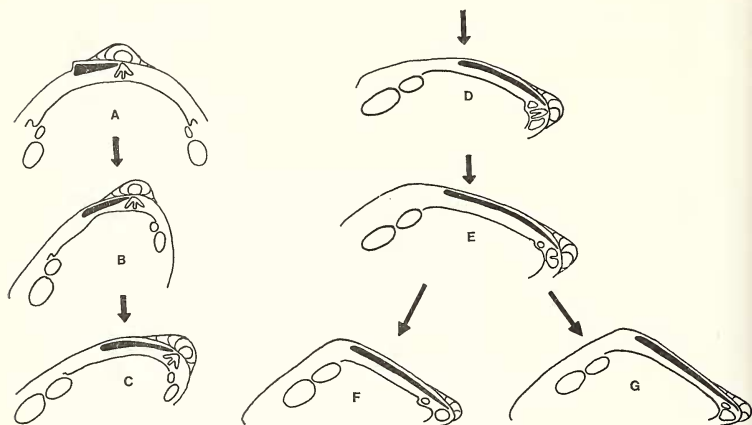
TEXT-FIG. 8. Diagram showing the possible course of evolution of the heteromyarian form in the
Dreissenacea, from an isomyarian ancestor. A, *Corbicula*; B, *Villorita*; C, Hypothetical; D, *Dreissenomya*;
E, *Congeria zsigmondyi*; F *Mytilopsis*; G, *Dreissena polymorpha*.

Dreissenomya aperta (text-figs. 2, 8D) possesses a rectangular-shaped shell, in which
the anterior (ventral) margin has only a small degree of flattening, whereas the posterior
(dorsal) margin is extended, with elongation of the ligament and enlargement of the
posterior adductor and posterior byssal and/or pedal retractor muscles. In addition
there is a well-defined pallial sinus, indicating that the animal had long siphons, and
was therefore adapted to an infaunal mode of life. Anteriorly the presence of a byssal
notch shows that the animal was attached to the substratum. The coexistence of a
pallial sinus and byssal notch can perhaps be explained by the animal living attached
to a solid substratum, but either partly or wholly buried by a surface covering of mud
or silt. Yonge and Campbell (1968) noted that *Dreissena polymorpha*, although attached
to stones by its byssus, is frequently found covered in mud and silt, alive and well.
Situated on the hinge plate of *Dreissenomya* are the scars of the anterior muscular
system, the anterior adductor muscle lying over and below (anterior to) the most
anterior of the two cardinal teeth. Above (posterior to) the cardinal teeth is the muscle

scar that represents the site of insertion of the anterior byssal and/or pedal retractor muscles.

The neotenous retention of the byssus in the ancestors of the Dreissenacea and the Corbiculacea must also have had an accompanying effect upon the relative importance of the pedal retractor muscles. Whereas in the burrowing Corbiculacea pedal retractors were necessary for the movements of the foot associated with burrowing, in the essentially epifaunal Dreissenacea their importance is diminished as the foot has ceased to be an organ of locomotion [except for the first year of life (Morton 1969c)] and is now merely used as a tool for the planting of byssal threads. In order for the byssus to fulfil its function as an anchor to the animal, enlargement of the byssal retractor muscles has occurred. It seems possible that the retention of the byssus in the ancestors of the Dreissenacea also resulted in a change in importance of different areas of mesoderm, so that the emphasis was displaced from development of pedal retractors to development of byssal retractors. Yonge (1962) showed that a small byssal gland is present in certain members of the Sphaeriacea. Assuming that this gland possesses at least a presumptive muscle mesoderm, then it is no big step to accept the view that the retention of the byssus caused preferential development of byssal muscles instead of pedal muscles in the ancestors of the Dreissenacea.

Congeria subglobosa shows another facet of the development of the heteromyarian form in the Dreissenacea. The shell is almost square in outline, and extremely solid. It seems unlikely that this bivalve could lead an epifaunal mode of life, since, although possessing a byssus, movement of water would put a great strain upon the byssal apparatus. The animal was probably attached to stones, but was covered by mud or silt. The anterior adductor muscle scar (text-fig. 3) surrounds a vestigial cardinal tooth, whilst the muscle scar of the anterior byssal and/or pedal retractor muscle is situated slightly further posteriorly than in *Dreissenomya*. Ventral flattening of an animal similar to *C. subglobosa* would result in the hypothetical creation of a form very similar to the living Dreissenacea. Perhaps representing a stage in the development of this form is *C. zsigmondyi*, in which the ventral margin of the shell is very much flatter (text-fig. 4), although the animal was in all probability a burrower. The anterior adductor muscle scar occupies the now familiar position underneath the umbo, whilst the anterior byssal and/or pedal retractor muscle scar is situated on a 'hinge lobe' projecting down from the hinge plate. Apart from the lack of ventral flattening this animal is very similar to *Mytilopsis* (text-fig. 7). Ventral flattening has been accomplished in *Congeria triangularis* (text-fig. 6) resulting in a form very similar to *Mytilopsis*.

Congeria subcarinata botenica (text-fig. 5), however, although flattened ventrally, is slightly different from *C. zsigmondyi* and *C. triangularis* in that the muscle scar of the anterior byssal retractor is not situated on a 'hinge lobe' but on the hinge plate itself near the anterior adductor muscle scar, a situation very similar to that in *Dreissena polymorpha* (text-fig. 1). It would seem that in the Dreissenacea, the positioning of the insertion of the anterior byssal retractor muscle has proceeded in two separate ways. Text-fig. 8 indicates a possible way in which the heteromyarian form could have evolved in the Dreissenacea. From a corbiculid type, e.g. *Corbicula* (text-fig. 8A), the elongation of the posterior border of the shell (caused not by the retention of the byssus, but probably so as to give greater efficiency in feeding whilst burrowing) has resulted in a form characterized by *Villorita* (text-fig. 8B) in which the evolutionary modification

of the anterior adductor muscular system has begun. This condition is extended in a hypothetical stage (text-fig. 8c) in which the progressive elongation of the posterior border of the shell and reduction in the anterior border has brought the anterior muscles on to the hinge plate and nearer the umbo. The effect of the neotenous retention of the byssus upon such an animal would have enhanced the evolutionary changes already started in the Corbiculacea, and perhaps produce a whole range of animals all basically pre-adapted to the future development of an epifaunal mode of life. Most became extinct, and only a few species have survived to the present day.

Dreissenomya (text-fig. 8D) and *Congeria zsigmondyi* (text-fig 8E) are extinct forms that show the way in which the heteromyarian condition could have evolved in the Dreissenacea. The insertion of the anterior byssal retractor on the hinge plate itself in such fossils as *C. subglobosa* and *C. subcarinata botenica* and present-day *Dreissena polymorpha* (text-fig. 8G) probably marks an evolutionary divergence from such forms as *C. zsigmondyi*, *C. triangularis* and present-day species of *Mytilopsis* (text-fig. 8F), in which the insertion of this muscle has progressed even further posteriorly along the hinge plate, with the formation of a 'hinge lobe' specially for its insertion. This adaption undoubtedly improves the efficiency of action of the byssal retractor. It is significant in separating *Dreissena* from *Mytilopsis*.

The evolution of the heteromyarian condition in the Dreissenacea is presumed to have taken place under conditions that differed from those in which *Dreissena* now lives. Yonge and Campbell (1968) suggested that it probably occurred in the intertidal or shallow sublittoral regions in the sea and that subsequently acquired powers of osmoregulation allowed the animals to migrate up rivers into fresh waters. Morton (1969a) supported this view. It is envisaged that the marine ancestor of both the Corbiculacea and the Dreissenacea underwent adaptive radiation, producing a wide range of forms capable of surviving in a variety of habitats. The ancestors of the present day Veneracea and Glossacea remained in the sea, while the ancestors of the Corbiculacea and Dreissenacea invaded estuaries, and there underwent further radiation. During their period in the sea the ancestors of the Corbiculacea and Dreissenacea left some forms on the sea-shore, e.g. *Mytilopsis*, and in estuaries, e.g. *Dreissena* (Morton 1969b), *Corbicula japonica* (Fuji 1957), and *Villorita cyprinoides* (Dinamani 1957). *Dreissena* has, in some localities, also invaded fresh waters, where it is ideally adapted to the exploitation of rocky surfaces. *D. polymorpha* is probably as cosmopolitan in the fresh waters of the Old World as *Mytilus* is in the seas. The fossil infaunal Dreissenacea probably represent distant relatives of *Dreissena* and *Mytilopsis* which reflect the evolutionary trend in these two forms. The evolution of the Corbiculacea and Dreissenacea in many ways parallels the evolution within the Unionacea, both groups having given rise to burrowing forms, e.g. *Sphaerium* and *Anodonta*, and epifaunal forms, e.g. *Dreissena* and *Etheria*.

The heteromyarian condition in present day Dreissenacea is a direct consequence of the evolutionary trend described which, it is suggested, proceeded from an established eulamellibranch stock. Available evidence suggests that the ancestors of the modern corbiculids gave rise to forms which ultimately produced the species of *Mytilopsis*, and *Dreissena polymorpha*. The neotenous retention in these genera of primitive characters, e.g. the byssus and a free swimming veliger larva, has made them extremely successful in the exploitation of rocky surfaces of fresh and estuarine waters. The evolution of the

heteromyarian form in the Dreissenacea mirrors in many ways the evolution of the same form in the filibranch Mytilacea.

Summary. It is considered that the evolution of the heteromyarian form in the Dreissenacea, culminating in the evolution of such recent forms as *Dreissena polymorpha* and species of *Mytilopsis* has taken place comparatively recently and from established eulamellibranch stock.

The neotenous retention of the byssus in forms ancestral to the modern Corbiculacea has contributed the greatest influence to this process. The effect of this process upon the ancestral isomyarian parent stock has been:

1. The extension of the posterior border of the shell, and ligament.
2. Reduction of the anterior (ventral) border.
3. Passage of the anterior adductor muscle and anterior byssal and/or pedal retractor muscles on to the hinge plate, with a corresponding reduction in the development of the cardinal teeth.
4. The relatively greater development of the posterior adductor and posterior byssal and/or pedal retractor muscles.
5. An increase in importance of the byssal retractors compared with the pedal retractors.

Stages in this evolutionary transition from an isomyarian to a heteromyarian form can be seen in fossil Dreissenacea.

Key to lettering

AA	Anterior adductor muscle scar
AB/PR	Anterior byssal and/or pedal retractor muscle scar
ABR	Anterior byssal retractor muscle scar
B	Byssal notch
H	Hinge plate
L	Ligament
PA	Posterior adductor muscle scar
PB/PR	Posterior byssal and/or pedal retractor muscle scar
PBR	Posterior byssal retractor muscle scar
PL	Pallial line
PS	Pallial sinus
T	Cardinal tooth
U	Umbo

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